Adapting to Environmental Heterogeneity: Selection and Radiation

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Abstract

Environmental heterogeneity is invoked as a key explanatory factor in the adaptive evolution of a surprisingly wide range of phenomena. This article aims to analyze this explanatory scheme of categorizing traits or properties as adaptations to environmental heterogeneity ("heterogeneity adaptations"). First it is suggested that this scheme can be understood as a reaction to how heterogeneity adaptations were discounted or ignored in the Modern Synthesis. Then a positive account is proposed, distinguishing between two broad categories of adaptation to environmental heterogeneity: properties selected for by well-defined patterns of environmental heterogeneity, and properties that help organisms exploit novel patterns of environmental heterogeneity.

Keywords

Adaptation; Environmental heterogeneity; Environmental novelty; Selective environment; Adaptive radiation.

1. Introduction

Paradigmatic cases of evolution by natural selection are typically represented as processes of adaptation to fixed environmental states. For instance, natural selection on Kettlewell's moths occurred in an environment defined by one of two environmental states, sooted or non-sooted trees (Kettlewell 1955), and individual moths were assumed to be either adaptive to sooted environments, or non-sooted environments, but not a mixture of both. Alternatively, consider how Darwin illustrated the theory of natural selection by describing how different varieties of wolf might adapt to one of two environmental states: mountainous habitats or lowland habitats (Darwin 2008, p. 70). Such paradigmatic examples of adaptation to environments defined by fixed states form the backbone of contemporary introductory textbooks on the subject (see for instance: Ridley 2004, p. 75; Futuyma and Kirkpatrick 2017, pp. 55–56).

While no biologist would deny that natural environments are much more complicated than such textbook models, such paradigmatic models can exert undue influence on how observations are characterized. For instance, observations of phenotypic plasticity were for a long time typically characterized as developmental noise. In 1965 Bradshaw complained about how phenotypic plasticity was too often interpreted as a "lack of stability" in development (Bradshaw 1965, pp. 115–116). More recently, Pigliucci similarly complained that plasticity was still too often considered an empirical "nuisance" and understood to be "simply a fancy word to indicate the old 'environment component of the phenotype'" (Pigliucci 2010, p. 355).

The work of biologists such as Bradshaw or Pigliucci serves to underscore a general insight: how environmental heterogeneity (change over time/space) is not only a source of evolutionary contingency (compare with Beatty 1995), but can also be a source of selection pressures, for instance favoring plasticity in a particular trait over more canalized development. Properties or traits are not necessarily only adaptive to fixed environmental states, but can also be "heterogeneity adaptations": adaptive to environmental heterogeneity.

This article aims to problematize heterogeneity adaptations, for it is less clear than may seem at first what is meant by categorizing some property or trait to be adaptive to "environmental heterogeneity" (EH). Some have understood EH very broadly, especially in the context of the evolution of cognition: general cognitive properties and even cognition itself

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have been hypothesized to be adaptive to EH as such.[1] Others, such as Pigliucci, have been at pains to emphasize how heterogeneity adaptations such as phenotypic plasticity cannot be adaptive to EH as such, but only to certain spatiotemporal patterns of EH (Pigliucci 2001).

If one broadens one's view, literatures on evolutionary transitions (eukaryotes, multicellularity, sex) or on the evolution of fundamental ecological interactions (metabolic exchange, motility, predation, cooperation, communication) seem to often (implicitly) partially explain traits or properties as adaptations to environments that are termed "heterogeneous" – or near-synonyms such as "variable," "complex," "structured," "noisy," "unpredictable." Table 1 gives a short overview of how a vast array of traits and properties is hypothesized as adaptive to EH.

Trait/Property	*Adaptive to*
Homeostasis	"Changing internal or external environment" (Cohen et al. 2012); noisy environments (Woods and Wilson 2013)
Motility	Environments that are "physically structured in such a way that nutrients are not equally available to all cells" (Wei et al. 2011, p. 4047.); "heterogeneous environments" (Fenchel 2002)
Intraspecific predation	"Environments characterized by large fluctuations in food resources," boom and bust dynamics with abundance and depletion (Polis 1981, p. 234)
Cooperation	"Unpredictable environments" (Jarvis et al. 1994; Avilés 1999); "Spatially structured environments" (Chao and Levin 1981; Nowak and May 1992)
Multicellularity	"Spatially structured" environments (Pfeiffer and Bonhoeffer 2003)
Polymorphism	Pattern of the environment in space and time (Levins 1968, p. 10)
Sex	"Overall environmental heterogeneity" (i.e., both biotic and abiotic, spatial and temporal) (Toman and Flegr 2018)
Plasticity	"Environmental variation in time or space" (Schmalhausen 1949; Bradshaw 1965; Lively 1986, building on Levins 1968)
Quorum sensing	"Fluctuations in cell-population density" (Miller and Bassler 2001)
Cognition	"Environmental complexity" (Godfrey-Smith 1996)
Brains	"Environmental variation" (Allman 1999, p. 2)
General intelligence (*g*)	"Evolutionary novelty" (Byrne 1995; Kanazawa 2004)
Cultural learning	"Fluctuating environments"; "moderate autocorrelation" (Boyd and Richerson 1985)

Table 1 The range of properties (both of individuals and populations) currently hypothesized to be adaptive to environmental heterogeneity.[2]

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[1] Consider, for instance, Godfrey-Smith's environmental complexity thesis: "The function of cognition is to enable the agent to deal with environmental complexity" (Godfrey-Smith 1996). Or consider Kanazawa's hypothesis that general intelligence (*g*) is an adaptation to "novel" environmental conditions (Kanazawa 2004).
[2] Not all explanations are explicitly labeled as "adaptive" by the authors: when authors have claimed that EH (or some related concept) is the "ecological" or "environmental" condition that explains the evolution of the explanandum, I have interpreted such explanations as adaptive explanations.

The challenge today, unlike for Bradshaw in 1965, is not to rehabilitate the significance of heterogeneity adaptations, but rather to gain more conceptual clarity on what heterogeneity adaptations should mean. While Table 1 should not be overinterpreted – it says nothing about how widespread the references to EH are, nor about the context in which it occurs – it does, at the very least, suggest that explanations that categorize traits/properties as "heterogeneity adaptations" should receive some more analysis. What does it mean for a trait or organism to adapt to environmental heterogeneity? Hence, one can ask how precisely the following explanatory scheme should be understood:

> The evolution of property P ("heterogeneity adaptation") can be partially explained by P being adaptive to EH. (CG)

The puzzle here is that, on the one hand, the coarse-grained scheme (CG) seems to pick out a prima facie plausible way of thinking about adaptations to EH. Yet, on the other, environmental heterogeneity is a broad, amorphous category, strictly speaking referring to all natural environments. Since explanatory schemes often leave out significant information (cf. Van Fraassen 1980), the question then becomes: where does the explanatoriness of (CG) lie?

In bringing attention to heterogeneity adaptations, this article aims to, on the one hand, situate their role within the larger development of the Extended Evolutionary Synthesis (EES), and on the other hand, to offer an analysis of the explanatory logic of explanations as schematized by (CG). In particular, a distinction will be made between two types of adaptation to EH: a process of natural selection in a well-defined selective environment, and a radiative process where the adaptative trait allows a novel resource to be exploited.

The article is structured as follows. In the next section, further motivation and background is given to the central question: how precisely are heterogeneity adaptations hypothesized across literatures, and why should one enquire as to the logic of the associated explanations? In the third section, the scheme (CG) is contrasted with how EH was treated by adaptive explanations in the Modern Synthesis, and it is suggested that a different approach to heterogeneity adaptations is an important part of the innovativeness of the EES. The fourth section builds on the pioneering work of Levins (1968), and sketches how precisely defined patterns of EH constitute the selective environment. The subsequent section argues that this does not exhaust the concept of heterogeneity adaptation: some traits or properties are adaptive to EH without a process of selection being responsible for that adaptiveness.

2. Adaptation and the Ubiquity of Environmental Heterogeneity

To give a sense of how EH features in a broad range of eco-evolutionary explanations, consider some leading hypotheses of how motility, predation, or multicellularity evolved. For instance, studies and simulations explicitly refer to heterogeneity in nutrients (over time and/or space) as a condition for motile organisms having a selective advantage over sessile organisms (e.g., Wei et al. 2011). The reasoning behind such studies is, roughly, that motility represents a spreading of the risk associated with each location. Even when motility is undirected (i.e., the organism moves randomly), on average organisms can avoid low-nutrient areas: this strategy outperforms sessile strategies when there is sufficient change in nutrient density over time. A second, related process that is sometimes cited as favoring motility is that motility can be a means to avoid competition (Hibbing et al. 2010): thus motility is not only a response to heterogeneity in abiotic variables such as nutrients, but can also be a response to specifically biotic variables.

Motility is one of the oldest adaptations to EH, but the ecological strategy of predation is also very old, having evolved numerous times among bacteria (Jurkevitch and Davidov 2007; Pérez et al. 2016). Moreover, while predation is a paradigmatically noncooperative interaction, some forms of predation are not easily distinguishable from symbiotic interactions: for instance, when a protist grazer becomes enveloped within a larger host, it can be difficult to say whether this is an instance of epibiotic predation (i.e., predation by enveloping the prey) or of endosymbiosis (López-García et al. 2017). Intraspecific predation (i.e., cannibalism) in particular has explicitly been hypothesized to be an adaptation to boom-bust dynamics abundance and depletion (Polis 1981, p. 234).

Further illustrating the sometimes indistinguishability of predation and cooperation, the two leading hypotheses on the origin of eukaryotes are that they occurred either through phagy (i.e., predation) or through symbiosis of plasmids or mitochondria (see Blackstone 2016 or O'Malley 2010).[3] Regardless of which hypothesis is the correct one, in either case Blackstone notes in a review of the subject (Blackstone 2013) that eukaryotes may have enjoyed a selective advantage over prokaryotes in part due to their much greater mobility, partially due to their much larger body size allowing for lower Reynolds numbers and thus less encumbrance by

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[3] An alternative hypothesis is that prokaryotes and eukaryotes have a common ancestor that was neither a prokaryote nor an eukaryote (Forterre 2013). Forterre proposes that "the ancestors of archaea (and bacteria) escaped protoeukaryotic predators by invading high temperature biotopes, triggering their reductive evolution toward the 'prokaryotic' phenotype" (Forterre 2013, p. 1).

viscosity. Eukaryotes are also hypothesized to be able to exploit "more or different" nutrients compared to prokaryotes (Blackstone 2013, p. 2): another instance of how predation and/or cooperation are adaptive to EH.

Greater body size and motility are hypothesized as key explanatory factors for why multicellularity arose (Schirrmeister et al. 2011). Greater cooperation (symbiosis) is another: multicellularity allows for cooperative hunting, cooperation for excretion of enzymes, or cooperation to produce antipredator toxins (Pfeiffer and Bonhoeffer 2003). For instance, one of the most basic transitions to multicellularity involves cooperating predatory *Myxococcus* bacteria (Grosberg and Strathmann 2007; Berleman and Kirby 2009).

As these hypotheses are advanced – either formally via experiment and simulation, or informally as a background explanation to help make sense of why some trait/property evolved – an explanatory structure emerges similar to the one familiar in the evolution of plasticity literature, where one of two rival traits/properties (plastic versus fixed, motile versus sessile, predatory versus grazing, multicellular versus unicellular) is favored in conditions of environmental heterogeneity. The question naturally emerges why this explanatory structure seems to be so versatile, especially given how heterogeneity is a quasi-metaphysical and ubiquitous property of natural environments.

To emphasize why this question should be posed, consider how adaptation is commonly construed as an adaptation to a specific "factor" in the environment (see, for instance, the "feature-factor" relationships in Bock 1980). When adaptation to EH is then considered (e.g., in the literature on phenotypic plasticity), it is analyzed as a simple variation (e.g., on/off) on a single factor. This common way of representing adaptation – as a feature-factor relationship – gives the misleading impression that there are two types of adaptation: adaptations to fixed factors, and adaptations to EH. Yet, as will now be argued, such "factors" are themselves idealizations of patterns of EH. Every adaptation is an adaptation to EH.

For instance, in Darwin's distinction between "mountainous" and "lowland" habitats, the label "mountainous" in reality refers to a pattern of fluctuation of altitude, vegetation, competitors, prey, and so on. In other words, a species of wolf adapted to mountainous habitats is adapted to a particular pattern of heterogeneity across a number of different environmental variables. Thus, strictly speaking, every trait or property that is adaptive to any environmental "factor" is in fact adaptive to a particular pattern of EH.

It is unclear what, if any, "feature-factor" relationship could not be analyzed in this way. In fact, the very existence of an organism entails a heterogeneity between the environment within the organism and the environmental external to the organism. Thermodynamic

equilibrium is by definition incompatible with life: not only does the existence of organisms entail a gradient, but to persist organisms need gradients in various variables. Even the basic (and likely essential) property of metabolism involves the organism feeding on gradients in chemical elements (iron, zinc, phosphorus, etc.) and creating novel gradients. For instance, bacteria consume both oxygen and H_2S, and thus can create steep gradients in these compounds over short spatial scales (Fenchel 2002). Interestingly, these waste products can, in turn, be consumed by other species as metabolic inputs (Fenchel 2002).

Of course, it may be justified to abstract away from patterns of EH: the precise fine-grained patterns of fluctuation within mountainous habitats may not matter when explaining why a certain variety or species of wolf is adapted to those habitats (as opposed to another variety/species). Similarly, iron is central to the metabolism of almost every living creature, and in fact iron metabolic pathways are almost ubiquitous across all phylogenies (Frausto da Silva and Williams 2001, pp. 512ff). So any model of the adaptive evolution of two wolf varieties will not need to take into consideration the micro-fluctuations in iron density: the two varieties both have robust iron metabolism so that patterns in iron fluctuation will likely not cause fitness differences. (By contrast, micro-fluctuations in iron density may be important for the evolution of some prokaryote lineages.)

The lesson here is not the complexity of natural environments cannot be idealized for certain explanatory ends, but that EH is ubiquitous in natural environments. There are no "factors" in natural environments. In a sense this lesson is simply a restatement of the core insight of process ontology (Dupré 2012): heterogeneity is a quasi-metaphysical property, reflecting the processual nature of environments. The processual nature may be safely ignored in many adaptive explanations, but only because the adaptations to those processes are very widespread and hence do not affect fitness differences between organisms.

In sum, adaptation to heterogeneity seems to play an intriguing role in explanations of the evolution of basic ecological strategies (motility, predation, etc.) and of the evolution of evolutionary transitions (eukaryotes, multicellularity). Yet, upon closer reflection, a "fixed environmental factor" simply is an idealization of a dynamic process, and so every trait is adaptive to some pattern of EH. So what does it mean to explain a trait or property as adaptive to EH, and why is it explanatory?

3. Adaptations to EH and the Modern Synthesis

Part of the story here is how the adaptive significance of EH was discounted in the Modern Synthesis. One instance of this discounting, as mentioned in the introduction, is well-documented in how the adaptiveness of plasticity was relatively ignored in the Modern Synthesis (see, e.g., Pigliucci 2006 or Pigliucci and Müller 2010). However, the discounting can be generalized to how the environmental heterogeneity was approached in the Modern Synthesis.

There is much controversy about the meanings of the terms "Modern Synthesis" and "Extended Evolutionary Synthesis," but for purposes here the former will be understood as a *vision* of biological evolution, where evolution is conceived as the change in allele frequencies through mutation, selection, drift, and migration. In other words, it is a vision of evolution where the paradigm is the theoretical framework of population genetics.

To understand the role of EH in this vision, it is instructive to recall one of the central explanatory interests of population genetics: the mapping of patterns of heredity between generations. Historically this explanatory interest was tied up with one of the core goals of eugenics, namely, the "the conscious social direction of human biological evolution" (Muller 1935, p. 41; cited in Kevles 1985, p. 176). {Citation}Thus for instance, it is no coincidence that more than a third of Fisher's monumental *The Genetical Theory of Natural Selection* (Fisher 1930) was dedicated to the socioeconomic and eugenicist implications of his mathematical synthesis of Mendelism with Darwin's theory of natural selection. The hope here was that, once the patterns of heredity were understood, one could shape the phenotypes of future generations by selecting which individuals of the current generation would reproduce. In other words, understanding heredity would allow for "better" artificial selection, through measures ranging from anticonception and marriage laws, to forced sterilization and other more extreme measures.

This explanatory focus influenced how environmental heterogeneity was conceived in adaptive explanations. Altering the environment (i.e., creating EH) was viewed as important to control selection pressures, and thus direct human evolution. However, here the patterns of EH were not viewed as occasioning specific selection pressures, but rather as creating different selection pressures over time. In other words, heterogeneity in the external environment (variation in the factors affecting fitness) was viewed as corresponding to heterogeneity in the selective environment (variation in selection pressures).

This explanatory interest in heredity helps explain why EH was often approached as an interfering factor to be minimized. One of the main types of experimental investigation into patterns of heredity of traits is known as "common garden experiments" where trait distributions in a parent and offspring populations inhabiting a common garden are compared. Such experiments aim at minimizing environmental heterogeneity ($V_E, V_{G \times E}$), so that phenotypic variation could be attributed to genetic variation:

$$V_P = V_G + V_E + V_{G \times E} + r = V_G + r$$

where the rest term r refers to all residual unexplained variations. Mapping the genetic basis of phenotypic variation (V_G) then allows for the classic questions of population genetics to be addressed: e.g., how alleles at different loci interact to produce phenotypes (e.g., epistasis), or how alleles at the same locus interact to produce a phenotype (dominance, codominance, incomplete dominance). Without eliminating the environmental component of phenotypic variation, these questions cannot be answered. For instance, if a phenotypic trait is not transmitted from one generation to the next, it becomes unclear whether this is due to dominance effects, or due to the offspring developing in a different environment. These difficulties remain present in the genomic era (de Villemereuil et al. 2016).

One of the first departures from this theoretical treatment of EH was Bradshaw's assertion that phenotypic variation due to environmental heterogeneity was too often being explained as developmental noise. Instead, some phenotypic variation was claimed to be adaptive to EH:

> <BQ>Much of the evidence has taken the viewpoint that stability and adaptation are correlated, and that lack of stability indicates lack of adaptation. […] But […] it seems that plasticity, or lack of stability, can be of positive adaptive value in many circumstances. (Bradshaw 1965, pp. 115–116)<BQ>

Considering this historical background of the explanatory goals and conceptual framework of the Modern Synthesis, this suggests that environmental heterogeneity is primarily conceptualized in the Modern Synthesis as a source of contingency, producing variable selection pressures.

In sum, if one considers how EH was approached within the Modern Synthesis, the coarse-grained explanatory scheme – i.e., explaining a trait as adaptive to EH as such – can be interpreted as signaling a departure from the Modern Synthesis. Hypothesizing a trait or property to be a heterogeneity adaptation is, in a sense, to categorize it as a non-textbook (NT) adaptation: the role of EH cannot be abstracted away, and the environment cannot be conceptualized in terms of feature-factor relationships. This suggests the following contrastive
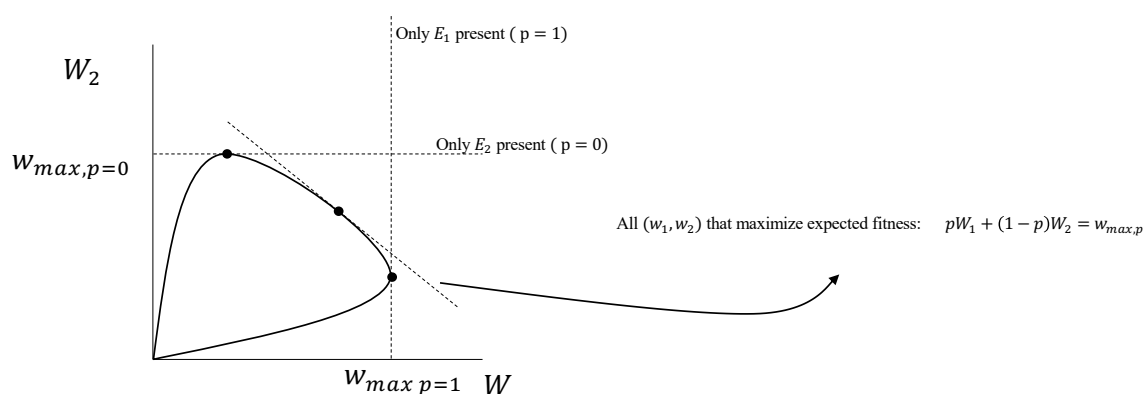
reading of the CG-scheme:

> The evolution of property P ("heterogeneity adaptation") can be partially explained by P being adaptive to EH, and not to any fixed environmental state.　　　　　　(NT)

4. Selective Heterogeneity

The scheme (NT) can help situate heterogeneity adaptations with respect to the EES, but as such it does not do much to help clarify the explanatory logic of categorizing properties/traits as heterogeneity adaptations. In this section I will recapitulate some of the core insights of Levins (1968), and sketch one major analysis of adaptation to EH.

4.1 Models of Selection for Heterogeneity Adaptations

Consider a continuous range of phenotypes with fitnesses W_1 when the environment is in state E_1 and fitnesses W_2 when the environment is in state E_2. These states can represent different states in condition variables (e.g., temperature), or in resource variables (high or low food availability, absence or presence of predators). A core assumption is that no single phenotype will maximize fitness in both environments: every phenotype involves some trade-offs in fitness. The mathematical construct that encapsulates this idea is the "fitness-set"[4] (see Fig. 1).

W_2

Only E_1 present (p = 1)

Only E_2 present (p = 0)

$w_{max,p=0}$

All (w_1, w_2) that maximize expected fitness: $\quad pW_1 + (1-p)W_2 = w_{max,p}$

$w_{max\ p=1}$　W

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[4] This is a reformulation of Levins (1968), but without discussion of the case of "fine-grained heterogeneity" (i.e., temporal heterogeneity shorter than generation time, and spatial heterogeneity smaller than habitat spatial scale). This is sufficient for purposes of this article; for more details see (Levins 1968, pp. 18ff).

Fig. 1 The fitness-set, given by the curve, for a range of phenotypes. Each point on this set represents a phenotype with a specific fitness trade-off

The figure includes three dashed lines: each represents the set of (theoretically) possible fitness trade-offs that maximize fitness when environments E_1 and E_2 occur with relative probabilities p and $(1 - p)$. The fitness set represents a constraint on what fitness trade-offs are actually possible, so the optimal fitness trade-off is given by the intersection of a dashed line with the fitness set. When only E_1 (or only E_2) occurs, the optimum is the fitness trade-off that maximizes W_1 (or W_2): a *specialized phenotype*. When E_1 and E_2 occur with relative probabilities p and $(1 - p)$, then the optimal tradeoff is determined by the intersection of the fitness set with the line $pW_1 + (1 - p)W_2 = w_{max, p}$ for maximal $w_{max, p}$. This is an *intermediate phenotype.*

In general, the optimal fitness trade-off is determined by the geometry of the fitness set, and in particular, its convexity or concavity. For a very convex fitness set (left graph in Fig. 2), even if the environment shifts from an E_1-dominated state ($p \approx 1$) to an E_2-dominated state ($p \approx 0$), the optimal fitness trade-off does not change much. In other words, specialized and intermediate phenotypes (or fitness trade-offs) do not differ much.
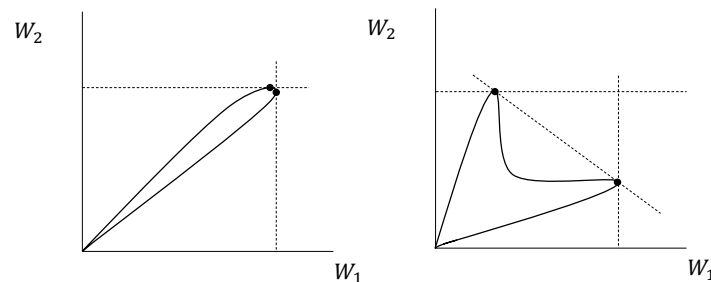
Fig. 2 A very convex fitness set (*left*) and a concave fitness set (*right*). In a very convex fitness set, large changes in the pattern of heterogeneity do not lead to large changes in the optimal fitness trade-off. In a concave fitness set, small changes in the pattern of heterogeneity can lead to discontinuous changes in the optimal fitness trade-off

By contrast, in a concave fitness set, such as the right graph in Fig. 2, there are no optimal intermediary states. Instead, as the environment shifts from an E_1-dominated state ($p \approx 1$) to an E_2-dominated state ($p \approx 0$), the optimal phenotype jumps discontinuously.

It is in a concave fitness set that environment-tracking can be optimal. Typical models of, for instance, the evolution of plasticity (e.g., Lively 1986; Moran 1992; Godfrey-Smith 1996) all take the relative frequency p of two environment types as a key parameter. Another important parameter is the probability of developing the adaptive phenotype in E_1 and E_2 (i.e., the probability of "making the right choice"). All such models identify cutoffs between situations where monomorphic specialization is optimal, and where flexible tracking is optimal. For instance, in Lively's model, E_1 and E_2 respectively represent benign and harsh patches. Here are clear conditions for the environment-tracking strategy being optimal (see Fig. 3, box a): the probability of making the right choice has to be large enough, and the probability of the benign patch occurring cannot be too high (because then it would be optimal to just ignore the occurrence of harsh patches).
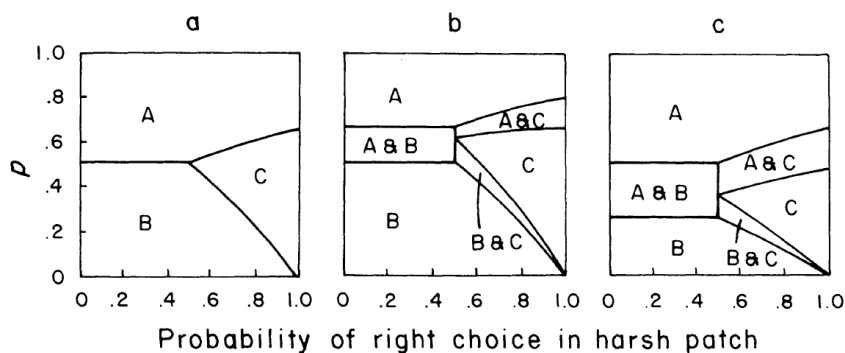

Fig. 3 (reproduced from Lively 1986, p. 658)

In Lively's model, intermediate phenotypes are never optimal, regardless of how often benign patches occur (i.e., the value of p). Instead, the choice is between monomorphic specialization (A or B), environmental tracking (C), or polymorphism (e.g., A and B, or A and C). The latter occurs in boxes b and c when competition between strategies is allowed.

The convexity or concavity of a set is a representation of the *tolerance* of specialized phenotypes (Levins 1968, pp. 17-18). The quantities $(w_{1,A} - w_{2,A})$ and $(w_{1,B} - w_{2,B})$ measure "how much worse" the specialized phenotypes do in the environment in which they are not specialized (see Fig. 4). When a specialized phenotype performs very poorly in an adverse environment, then tracking may be optimal, even though the latter may not do as well in benign

environments. The tolerance determines whether monomorphic or tracking/polymorphic strategies maximize fitness (e.g., Godfrey-Smith 1996, p. 211).
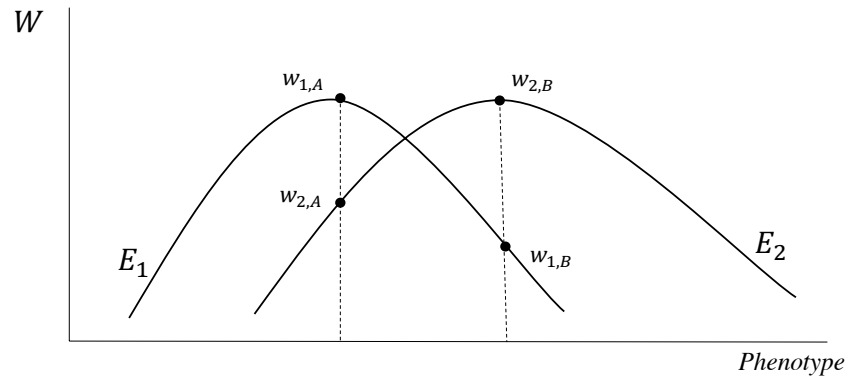
Fig. 4 Tolerance curves for a range of phenotypes in environments E_1 and E_2, with monomorphic specializations A and B

What determines whether polymorphism or environmental tracking is selectively favored depends on the spatiotemporal *scale* of heterogeneity, and specifically, whether the temporal scale exceeds generation time or the spatial scale exceeds the typical habitat range of an individual.[5] This means that an individual in the course of a lifetime will typically not encounter any EH, but a population will encounter EH. In the latter case, a mix of specialized phenotypes (i.e., polymorphism) is optimal; in the former, evolutionary tracking will be favored.

Note that models of selection for plasticity (e.g., Lively 1986; Moran 1992; Godfrey-Smith 1996) typically do not explicitly represent the tolerance of phenotypes or the scale of heterogeneity. Instead, they tend to focus on the reliability of cues: the probability that tracking will be accurate in various environments. However, the reliability of the cue is sometimes related to the temporal scale of EH: when the latter is shorter than the reaction time of the phenotype, the phenotype can never adapt on time. Thus, for instance, if the density of predators varies on a timescale that is shorter than the reaction time of the defenses of bryozoans, by the time the defenses are set up, the predators will be gone. The pattern of EH will effectively be just noise for the bryozoan.

Two lessons can be drawn from this technical discussion. The first lesson is that a main distinction among adaptations to EH is to be made between monomorphic phenotypes (either intermediate or specialized phenotypes) and tracking phenotypes. The second is that the

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[5] Levins terms this "coarse-grained" heterogeneity (Levins 1968, p. 18).

concept of a "pattern of EH" can be spelled out in detail, in terms of dimensions such as: (1) the geometry of fitness sets (containing information about environmental tolerance), (2) relative frequency of environment types, (3) spatiotemporal scale of EH, and (4) reliability of cues. To this could be added: (5) autocorrelation between environments across generations (how similar the parent environment is to the offspring environment: this adds a multigenerational timescale), and (6) the cross correlations between environmental variables. For purposes of this article, a "specific pattern of EH" can be understood to be a pattern definable by such dimensions.

4.2 Adapting to Selective Heterogeneity

The following analysis of the explanatory scheme (CG) can be proposed: when a property is explained as a heterogeneity adaptation, this can mean that the property was selectively favored in a selective environment characterized by a particular pattern of EH.

> The evolution of property P can be partially explained by P *selectively favored by a pattern of* EH.
>
> (SH)

Here it is the pattern of EH, and not the brute fact of EH, that is deemed explanatorily significant. The selective heterogeneity scheme (SH) also covers the previous scheme (NT), since adaptation to fixed environmental states can be analyzed as a special case of an adaptation to a pattern of EH. When the pattern matters, parameters such as the relative frequency of environmental states, or the spatiotemporal scale of variation matter. Other factors, such as autocorrelation, or cross-correlation between environmental variables also define the pattern of EH.

As an illustration, consider two environments: one is more or less stable, characterized by slow climate changes, and the second environment varies at seasonal rates. Type O_1 is adaptive to the first environment, while the second type O_2 is adaptive to the second. Figure 5 illustrates this situation, where X is some environmental variable (temperature, humidity, nutrition density). The average value of X is the same in both E_1 and E_2, but, from the perspective of the organism, in E_2 there is more uncertainty due to intragenerational change. The right graph in Figure 5 represents E_1 and E_2 as two selective environments with different selective regimes: O_1 is fitter in E_1 , and O_2 is fitter in E_2.
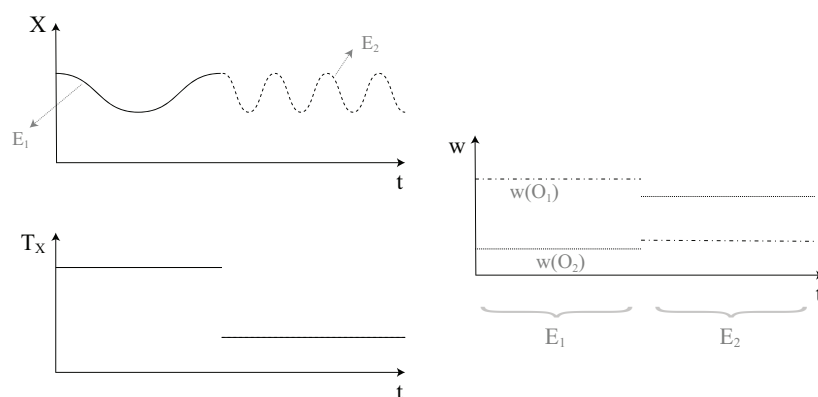
Fig. 5 Patterns of EH individuate selective environments

When one would claim O_2 as adaptive to EH – for instance, migratory behavior among birds is viewed as adaptive to EH (Rappole 2013) – then this claim is explanatory when a specific pattern of EH is intended (e.g., seasonal change).

The scheme (SH) can be further illustrated by applying it to some representative examples listed in Table 1:

- **Sexual reproduction** is adaptive to EH insofar as it is a *mixed strategy at the level of populations*.[6] Unlike polymorphism in a single trait, sexual reproduction can be explained as adaptive to heterogeneity in a large number of environmental variables.

- **Motility** is adaptive to EH insofar as it is a *mixed strategy at the level of the individual,* whereby location is varied randomly over time in order to maximize the probability of exposure to nutrient-rich locations (see Wei et al. 2011). Most mechanisms of motility involve some sensory system as well (e.g., chemotaxis), and such **sensorimotor systems** are strategies of *environment-tracking* (see, e.g., Fenchel 2002).

- **Phenotypic plasticity** is adaptive to EH insofar as it is a strategy of *environment-tracking*: as documented above, plasticity is adaptive to patterns of EH that exceed the tolerance of fixed phenotypes and with scales of fluctuation that are smaller than generation time or typical habitat size. Depending on further details of the pattern (autocorrelation of environments across generations) and interaction between

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[6] Adaptive strategies at the level of the individual are adaptive to the environment of individuals; whereas those at the level of the population are adaptive to the environment of the population. For our purposes here, the environment of the population can be understood to consist of the sum total of the environments of the individual.

individual and pattern (accuracy of cue, time lag of cue), different types of plasticity are optimal (for reference, see, e.g., Pigliucci 2001, p. 200).

- **Cognitive and proto-cognitive properties** are adaptive to EH insofar as they constitute a strategy of *environment-tracking at the level of individual.* Many analyses of the evolution of cognition draw heavily on the adaptive evolution of plasticity and/or sensorimotor systems. For instance, Godfrey-Smith's claim that cognition is adaptive to environmental complexity is supported by a model of the selection for single-trait phenotypic plasticity (Godfrey-Smith 1996). Accounts that analyze proto-cognition as sensorimotor capacities point to the latter as allowing an organism to "better adapt to rapidly changing environmental conditions" (van Duijn et al. 2006).

- **Cultural learning** is adaptive to patterned EH insofar it is a strategy of *environment-tracking at the level of population.* Adaptation via cultural learning is favored over adaptation via genetic change when the magnitude of EH at the timescales of multiple generations is sufficiently high, such that tolerances are exceeded (see Boyd and Richerson 1985, p. 111).

5. Radiative Heterogeneity

This final section identifies and explores a second kind of adaptation to environmental heterogeneity. Here the process of adaptation occurs without being caused by fitness differences or natural selection, for instance, when an organism encounters a novel exploitable resource and is the first to take advantage. The organism cannot, by definition, share a common selective environment with its rivals, because its fitness (but not theirs) is influenced by the novel resource. Hence the fitness differences are not commensurable: a prerequisite for a selective environment to be shared (Brandon 1990). The adaptive evolutionary process that ensues is that of adaptive radiation. Hence the type of EH that gives rise to this process is termed "radiative heterogeneity."

5.1 Novelty and the Limits of Selective Environments

As a concrete illustration of radiative heterogeneity, consider the following passage:

<BQ>A question that remains, however, is whether harsh demographic or ecological conditions are necessary for sociality to evolve. It is possible that sociality may also have arisen in species sitting comfortably in a region of sustainable growth, if, by cooperating, individuals could gain access to rich and otherwise inaccessible resources [...]. Potential examples of this second alternative are the conifer-bark beetles, which,

> by attacking en masse, are able to overcome the defenses of live trees […] and some of the cooperative hunters such as wolves […] and social spiders […], which by hunting in groups are able to gain access to a range of prey sizes unavailable to non-social species of a similar body size […]. (Avilés 1999, p. 470)<BQ>

In other words, here it is hypothesized (and for similar pictures of the evolution of cooperating beetles, see, e.g., Berryman et al. 1989 or Birch 1984) that the typical selection pressures associated with patterns of EH (harsh conditions, with patchy resources) were not necessary for the evolution of sociality. Instead, an environmental variable that had not previously impacted fitness values, namely the presence of live trees,[7] now is part of the external environment of groups of bark beetles due to a behavioral innovation. Sociality is adaptive to this novel pattern of EH, and the cooperating conifer-bark beetles will continue to evolve in this novel environment (and start competing with each other). Thus the exploitation of the resource leads to adaptive radiation.

Paradigmatic cases of adaptive radiation, like the radiation of Darwin's finches to different islands, involves physical migration to spatially distinct environments with different characteristics. However, a more general characterization of radiation is: "invading underexploited environments" (Grant 2013). In this way radiation can involve processes without any physical displacement, but can be caused by developmental, behavioral innovation, or evolutionary change, such as new sensory capacities being evolved, or larger body size allowing previously inaccessible resources to be exploited. While radiation involves evolutionary divergence of populations (e.g., speciation of an ancestral species into descendant species), radiation can sometimes be considered a process of "adaptation" in the sense that the radiating populations avail themselves of different "ecological opportunities" (Grant 2013, p. 561).

Inspired by this, the concept of radiative heterogeneity can be defined in the following way:

> **Radiative heterogeneity:** A pattern of EH in the external environment of an individual or population is *radiative* if: (1) it is novel, and (2) it does not constitute any selective environment of the individual or population.

Let us unpack this definition. First, stipulating that a radiative pattern of EH does not constitute any selective environment means that the pattern does not occasion any new selection pressures

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[7] More precisely: the fitness impact of live trees is "screened off" (sensu Salmon 1984) by the fitness impact of dead trees. So live trees qua live trees (and not just potential dead trees) were not part of the external environment.

or give rise to novel selection pressures. It *does* affect fitness (it can represent, for instance, an underexploited resource), but because the radiating population inhabits a different external environment, the fitness differences between radiating and non-radiating populations are not commensurable and hence do not constitute selection (on the short-term at least).

To give this some formal detail (Fig. 6): suppose that organism type O_3 gains sensitivity to fast variations in environmental variable X (e.g., intraday variation as opposed to slower seasonal variation). Assume for the sake of simplicity that these fast variations occur in a spatially distinct environment E_3. After evolving or developing the novel capacity, O_3 migrates to this (uninhabited) environment E_3.
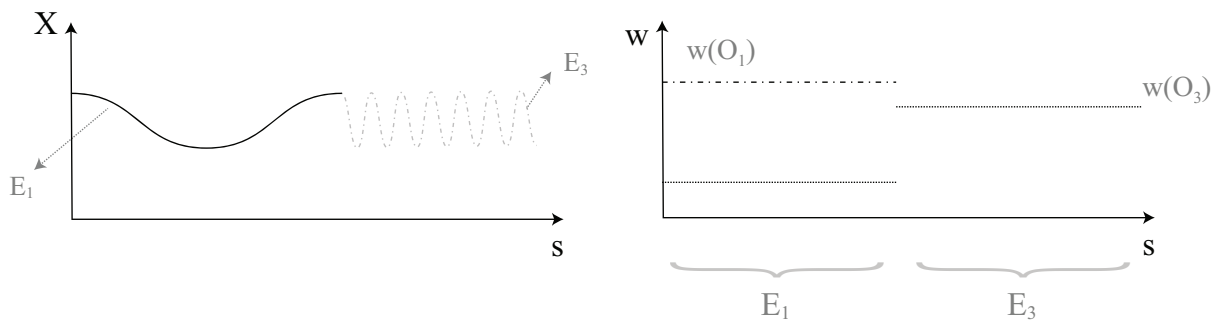
Fig. 6 An illustration of radiative heterogeneity (as a fast variation in X), and how organism O_3 is adapted to E_3 despite not having been selected for in environment E_3

Organism O_3 is adapted to E_3, even though there was not any selection process that led to this adaptiveness. The novel pattern was not part of O_3's previous selective environment (shared with O_1). In O_3's novel external environment (E_3), the concept of selective environment is not well-defined, since there are no fitness differences to speak of. Unlike the case of selective heterogeneity, radiative heterogeneity does not generate any specific selection pressures: it does not even make sense to ask what selective environment is associated with a pattern of radiative EH.

In general, adapting to radiative heterogeneity need not involve a preexisting calibrated response to a well-defined pattern of heterogeneity. Simply escaping selective competition, for instance by migrating outside of one's usual habitat, can be adaptive, and in this sense can be considered as an instance of adapting to radiative heterogeneity. Escaping a selective environment may be adaptive if the potential opportunity of the unencountered outweighs the potential risk, despite the precise pattern of EH being unknown. As previously mentioned, this is precisely how motility is sometimes considered to be an adaptation to EH.

This contrast between radiative and selective heterogeneity implicitly draws on the fact that the Lewontin conditions – heritable fitness differences in phenotype – are, strictly speaking, insufficient to characterize natural selection. To give an exaggerated example: fitness differences between peppered and black moths constitute natural selection, but fitness differences between orca and krill do not. The concept of selective environment is one way to account for why fitness differences between orca and krill are not commensurable: very different environmental processes determine their respective fitnesses. A pattern of radiative EH is a novel pattern that only part of the ancestral population can exploit, and hence the fitness of individuals in the ancestral population are not affected by the same environmental variables. In this way, the novel pattern cannot be considered as part of a common selective environment.

The other definitional element of radiative heterogeneity needing unpacking is the concept of environmental novelty. A full treatment of this concept would warrant a separate paper; it is sufficient for the purposes here to understand a novel pattern as a pattern that is part of the current external environment, but was not part of a previous external environment and so did not previously affect fitness. This is continuous with other definitions of environmental novelty, for instance, that of Sol et al. (2005) where novelty refers to "areas outside the natural geographic range of the species," and specifically to novel resources or unknown enemies in those areas.

The concept of novelty is relevant for understanding the example cooperating and noncooperating beetles (Avilés 1999). The property of "cooperation" allows the cooperating beetles to exploit a factor in the environment with which there had not been any previous direct interaction. This means that they do not entirely share a selective environment with the non-cooperating beetles. However, this is not to say that at a later stage there may be some selective competition: if the population size of cooperating beetles grows, then this could lead to subsequent displacement of noncooperating beetles. Nonetheless, initially, the adaption to environmental heterogeneity occurs without natural selection in a common selective environment. In this way the distribution of live trees represents an instance of radiative heterogeneity.

5.2 Adapting to Radiative Heterogeneity

Intuitively, adaptations to radiative heterogeneity simply allow for novel ecological opportunities to be exploited. However, the traits/properties discussed here go beyond traits such as the different beak sizes of Darwinian finches, but concern fundamental properties like motility or multicellularity: properties that characterize a broad swathe of phylogenies and that have colonized many habitats and niches. To account for the fundamental nature of radiative heterogeneity – and associated adaptations – three different types of radiative heterogeneity can be distinguished.

One type of radiative heterogeneity reflects the *spatiotemporal extension of resources*. This means that properties that allow organisms and populations to take advantage of the extension of resources – venturing outside a species' normal habitat range, migration, and so on – are adaptations. Habitat expansion means that the organism can avail itself of more, and more varied resources (food types, mating opportunities, etc.). As mentioned, this is why motility is considered adaptive, and thus motility is not only adaptive to selective heterogeneity (giving motile organisms a selective advantage), but also to radiative heterogeneity.

A second type of radiative heterogeneity reflects the *multidimensionality in resources* (the various types of food, shelter, potential cooperators, etc.), where not all potentially exploitable resources are actually exploitable by extant organisms. To revisit the external environment of bacterial life (second section): initially resources such as light and many of the chemical elements were not exploited by bacterial life forms. As life evolved more patterns of EH were exploited. For instance, the evolution of chlorophyll allowed for high-density regions of solar radiation to be exploited. Moreover, as life evolved, novel patterns of EH were created, as organisms created metabolic inputs for other organisms, either by their waste products or by their existence. The evolution of predation allowed for the exploitation of the latter.

A third type of radiative heterogeneity reflects the *multitude of existing patterns of EH*. Not only are environments characterized by a large number of resource types that are unevenly spread across space and time, but the distribution of these resource types follows intricate patterns that are often imperfectly regular and involve the superposition of many simple (i.e., sinusoidal) patterns. For instance, resident birds may pick up on complex patterns in resource distribution in their regular habitat; however, these distributions may change over time (for instance, due to seasonal change) and space (for instance, due to latitude). Migratory birds exploit these latter spatiotemporal patterns of heterogeneity, and in this way avian migration can be considered as an "adaptation" (e.g., Rappole 2013, p. 162). However, interestingly, migrant species usually do not directly compete with resident avian species, and are primarily in competition with other migrant species (cf. Rappole 2013, p. 160): the spatiotemporal pattern

of seasonal and latitudinal variation defines a novel selective environment in which different variants of migrant behavior are selected for.

Nonetheless, migrant and resident variants can still enter into competition, especially when resources are scarce. The reason for this is that seasonal variation is only adaptively significant because it is a *cue* for an already existing selective pattern of EH, namely (underexploited) food resources. In this way, this third type of radiative heterogeneity can be considered to refer to additional dimensions in exploitable resources: subtle undetected patterns represent an "informational resource" that can be exploited. This third type of radiative heterogeneity also reflects how the spatiotemporal distribution of resources involves the superposition of many simple patterns, and hence can be predictable to varying degrees. One organism type may be able to exploit slow, seasonal variation, whereas another organism type may be able to additionally exploit faster, diurnal variation.

More work would need to be done to formally analyze the category of "radiative heterogeneity" with the same precision as that with which selective heterogeneity was analyzed. However, even this short analysis is sufficient to suggest why so many very fundamental evolutionary innovations seem to be adaptive to radiative heterogeneity: radiative heterogeneity is ubiquitous and itself reflects fundamental physical properties of environmental resources, such as multidimensionality and spatiotemporal extension. An adaptation like motility directly takes advantage of spatiotemporal extension; an "adaptation" like cooperation allows access to novel resources and thus to take advantage of multidimensionality in the environment.

In sum, the coarse-grained explanatory scheme (CG) can be understood to refer not just to adaptations to selective heterogeneity, but also to adaptations to radiative heterogeneity:

> The evolution of property P ("heterogeneity adaptation") can be partially explained by P *allowing for exploiting radiative patterns of EH*   (RH)

The selective heterogeneity (SH) and radiative heterogeneity (RH) explanatory schemes are not mutually exclusive and can be applied to the same property; they just refer to distinct adaptive processes. In general, an adaptation to radiative EH may be used to gain a selective advantage, and adaptations to selective EH may be used to exploit novel resources. Motility, in that it allows bacteria to both avoid selective competition as well as occupy the most desirable positions, is a case in point.

The scheme (RH) can be further illustrated by applying it to some representative examples listed in Table 1:

- **Motility** is adaptive to radiative heterogeneity insofar as it allows escaping selective competition and/or colonizing novel patterns of EH. Bacterial motility is often used to gain a fitness advantage in a common selective environment – for instance, to gain access to more oxygenated or nutrient rich regions in biofilms (Hibbing et al. 2010, p. 7). This would be an instance of motility as an adaptation to selective heterogeneity. However, some bacterial strains have been noted to use motility to actively evade competition, and to disperse more rapidly into less occupied regions (Hibbing et al. 2010, p. 7). Here motility would be an adaptation to radiative heterogeneity.

- **Cooperation** is adaptive to radiative heterogeneity insofar as it allows colonizing novel patterns of EH. We already noted the example of cooperating bark beetles; cooperation is of course a widespread and biologically fundamental phenomenon. It lies at the basis of **multicellularity**, which has been hypothesized to have allowed for the exploration of new niches (Schirrmeister et al. 2011). Wolfpacks of cooperating predatory bacteria (*Myxococcus*) are considered to be a form of rudimentary multicellularity (e.g., Grosberg and Strathmann 2007), and exemplify in another way how motility also is adaptive to radiative heterogeneity.

- **Cultural learning** is adaptive to radiative heterogeneity insofar as it has allowed significant niche expansion in human evolutionary history. Culturally transmitted knowledge (e.g., about which roots are nutritious and which are toxic) as well as culturally mediated cooperative hunting allowed for dietary expansion, and this dietary expansion was one of the factors that allowed the geographic expansion of the human metapopulation (Teaford and Ungar 2000; Ulijaszek 2002). This dietary expansion also involved access to previously inaccessible food sources, such as big game through cooperative hunting. Innovations such as structured hearths, more sophisticated artificial shelters, and clothing allowed for buffering against periods of severe cold during glacial periods as well as migration to areas with cold climates (Gilligan 2007). Such properties, allowing populations to undergo niche evolution, were clearly not primarily a means to selectively compete with other populations, although they have been linked with some interspecific competition with, e.g., Neanderthals (cf. Gilligan 2007).

- **Endothermy** (a homeostatic process) is adaptive to radiative heterogeneity insofar as it allows colonizing novel patterns of EH. Endothermy allows mammals and birds to

be less affected by diurnal cycles in temperature than ectothermic organisms: they can keep on feeding without having to resort to "basking" behaviors or microhabitat selection (cf. Ruben 1995, p. 70). Hence endothermy is thought to have allowed for organisms to expand into new niches – areas with sparse resources requiring extended feeding periods, or areas with cold temperatures (Ruben 1995, p. 71).

6. Discussion and Conclusion

The main aim of the article was to draw attention to a relatively common explanatory scheme where traits/properties are explained as adaptations to environmental heterogeneity. Where the explanatory import lies is not obvious when one considers the ubiquity of environmental heterogeneity. Environmental heterogeneity is not special, so why invoke it in an adaptive explanation?

Part of the story, it was suggested, lies in the contrast with how adaptation is represented in textbooks as "feature-factor" relationships and with how EH was treated in the Modern Synthesis, namely as a source of contingency. It is now widely recognized that patterns of EH can occasion specific selection pressures, but perhaps it is still necessary to emphasize the contrast with depictions of adaptation in textbooks or in the Modern Synthesis.

However, the main positive contribution of the article was to propose the distinction between two types of environmental heterogeneity: selective heterogeneity, which serves to define specific selection pressures, and radiative heterogeneity, where EH functions as a resource that can be exploited by individuals and populations. Radiative heterogeneity, in particular, seems to be ubiquitous, and this helps to account for why the explanatory scheme of explaining traits/properties as heterogeneity adaptations is so versatile and widespread.

The notion of an adaptation to radiative heterogeneity raises interesting further questions that cannot be treated here. Adapting to radiative heterogeneity is, in the first instance, an ecological process; calling it an "adaptation" raises deeper questions as to how we should understand both the concept of adaptation and the link between adaptation and selection. On the one hand, adaptations such as cooperative behavior can "fit" factors in the external environment, such as the presence of live conifers. Evolutionary ecologists speak of "adaptations" when referring to a trait that allows for resource exploitation or niche colonization. Yet it is clear that adaptations to radiative heterogeneity cannot be analyzed as adaptations according to perhaps the most influential analysis of that concept, namely as a property that gives (or has given during some selective history) a fitness advantage in a given

selective environment (Williams 1966; Brandon 1978). Thus the question arises how this explanatory practice should be squared with canonical accounts of adaptation in the philosophy of biology.

Other questions could also be raised about how natural selection interacts with adaptations to radiative heterogeneity. It is clear that an adaptation to radiative heterogeneity can be used to gain a selective advantage. Motility, for instance, allows bacteria to explore novel niches but also to gain a selective advantage over nonmotile strains. Endothermy can allow for niche expansion, but can also allow for a selective advantage to be gained over ectotherm types in a common selective environment. Sometimes the selective advantage follows the niche expansion: does this mean that some selective environment was shared all along? While this is unclear, one can conclude that taking the default heterogeneity of environments into account does seem to cast concepts such as "adaptation" and "natural selection" in a different light.

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